Potential for lodgepole pine regeneration after mountain pine beetle attack in newly invaded Alberta stands

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A B S T R A C T

The range expansion of mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae)) from the focal region of the recent major epidemic in British Columbia, Canada to the north and east into Alberta's lodgepole pine forests may alter the future successional pathway of these forests. Thus, there is a need for an improved understanding of recruitment dynamics of lodgepole pine in both healthy and MPB-attacked stands arising from this shift from a fire-driven disturbance regime to a disturbance regime that also includes MPB. We evaluated the potential impacts of mountain pine beetle attack and associated forest management on the future regeneration potential of lodgepole pine forests in western Alberta. We quantified seedbed availability and advance regeneration, and compared lodgepole pine recruitment of sown seed on five different seedbed types (i.e., moss, shallow organic, deep organic, decayed wood, and mineral soil) within four different stand treatment types that simulated mountain pine beetle attack and forest management disturbance (i.e., control, moderate MPB attack, high intensity MPB attack, and salvage harvest) in the Upper Foothills of western Alberta. Recruitment from sown seed 1–3 years after MPB attack was poor (median 0%, 0–2% 5th–95th percentiles) across stand treatment types for moss and both organic seedbed types. Decayed wood and mineral soil were the best seedbed types, with higher recruitment rates than the organic and moss seedbeds, although recruitment was still relatively low (median 0%, 0–6% 5th–95th percentiles). Recruitment rates of seedlings on decayed wood and mineral soil seedbed types increased with increasing levels of disturbance; recruitment was lowest in control stands, higher in the simulated MPB-attack treatments, and highest in the salvage logged stands. However, these favorable seedbeds were scarce among all stand treatment types. Given the extremely low levels of advance regeneration and lack of natural regeneration we observed initially after MPB attack in our study sites, we anticipate that future stand development will be hampered by a lack of lodgepole pine recruitment, at least in the short term. If the goal is a re-stocked forest, significant silvicultural intervention will be required for lodgepole pine forests attacked by MPB within novel habitat ranges in western Alberta.

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1. Introduction

Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) forests have historically initiated as even-aged pioneer forests after stand-replacing wildfire. However, this historical disturbance regime is currently being altered, with increased impacts of disturbance by mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae)), which is actively expanding its range in western Canadian pine forests (Carroll et al., 2004; Nealis and Peter, 2008). MPB is considered the most destructive forest insect in western North America with a recent epidemic in British Columbia resulting in mortality of 710 million cubic me-

ters of timber over a cumulative affected area of ~18.1 million hectares and the area and impacts continue to grow (Furniss and Carolin, 1977; Safranyik and Carroll, 2006; BC, 2012). In 2005 MPB moved east across the Rocky Mountains and quickly spread through the extensive stands of boreal lodgepole pine in Alberta; attack in the novel host jack pine (*Pinus banksiana* Lamb.) has now also been confirmed (Cullingham et al., 2011). Continued expansion of MPB further east and north across the boreal is possible, although this will depend on suitable climate and host availability. The long-term implications of the expanding range of this disturbance agent are uncertain, but MPB is likely to remain in Alberta (Schneider et al., 2010).

MPB differs from other disturbance agents, including wildfire, windthrow, and timber harvest, in that it directly affects the over-story without disturbance to the understory, forest floor or soil (Burton, 2008). Severity of MPB mortality can range widely (0–

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100%) with environmental conditions (e.g., elevation, climate and topography), but in British Columbia, Canada (BC) MPB has resulted in mean overstory tree mortality in the range of 25–50% of the pine trees per stand (Shore et al., 2006). Serotiny provides a long-term canopy seed bank available for dispersal after disturbance. This seed can remain viable for an extended period of time in the cones (e.g., Ackerman, 1966; Teste et al., 2011b), with viability >30% possible even after 20+ years (Aoki et al., 2011). While we would expect cone serotiny to be detrimental to pine regeneration in the absence of fire, a BC study showed 45% of the canopy seed-bank was released via cone opening, breakage of cone-bearing limbs, and squirrel predation within 6 years of MPB attack, with a sustained seedbank release even 9 years after attack (Teste et al., 2011a). Thus, we do not expect the seed availability and viability to be limiting factors in the regeneration of lodgepole pine after MPB attack. However, the sustained longer-term release of seed in MPB disturbed stands, as compared to the synchronous release of seed from serotinous cones which occurs after fire disturbance, will have important implications for the post-disturbance development of these forests. More importantly, seedbed limitations and environmental conditions in the understory will likely be dominant factors influencing regeneration.

A better understanding of the availability of seedbeds favorable to lodgepole pine recruitment in MPB attacked stands, compared with both undisturbed and managed lodgepole pine forests is required (Dhar and Hawkins, 2011). Teste et al. (2011a) suggested that after MPB attack, either fire or anthropogenic disturbance would be needed for normal levels of pine regeneration to occur. Favorable germination microsites will depend on the availability of both suitable seedbeds for germination and survival of germinants, and the associated environmental conditions, including light availability (Wright et al., 2000), and soil moisture status (Despain, 2001). While lodgepole pine can regenerate on a wide range of seedbeds, it generally prefers mineral soil, decayed wood or disturbed organic material (Lotan, 1964; Nyland, 1998), which are unlikely to be dominant seedbeds in MPB attacked stands that have a predominately undisturbed forest floor (Astrup et al., 2008). Thus, unsalvaged beetle-killed stands may lack the ground disturbance needed to create a suitable seedbed for natural regeneration of lodgepole pine, and are likely to regenerate slowly with low densities (Mitchell, 2005).

Research in multiple regions has suggested that the pre-disturbance composition and dynamics of the advance regeneration seedling/sapling bank will play an important role in determining the future structure and dynamics of these forests after MPB attack (e.g., Collins et al., 2011). In some lodgepole pine forest types, advance regeneration includes sufficient lodgepole pine to meet stocking density guidelines for a new forest (e.g., FPBSR, 2007; Nigh et al., 2008 in BC; Diskin et al., 2011 in CO; Kayes and Tinker, 2012 in WY). However, in other lodgepole pine forest types, including those with mixed species composition, the advance regeneration often favors a shift towards later-seral shade-tolerant species such as spruce and fir (e.g., Vyse et al., 2009; see review by Dhar and Hawkins, 2011). Yet other studies have shown limited regeneration of any species after MPB attack (e.g., Astrup et al., 2008). For lodgepole pine forests without a seedling bank the future successional pathway is uncertain.

Management for MPB can range from individual tree removal to post-attack salvage harvest to managing for other objectives, such as watershed protection or wildfire fuel management, in areas where infestation levels are uncontrollable (ASRD, 2007). In salvage logged stands, serotinous cones on or near the ground open and release their seed when exposed to warm soil surface temperatures (Lotan, 1964), thus creating a short-term seed bank for natural regeneration (Ackerman, 1966) that can contribute to regeneration of fully-stocked lodgepole pine stands (e.g., Collins

et al., 2010). But given the magnitude of MPB attack and associated dead timber on the landscape, there may also be a large portion of the MPB-attacked landscape left unmanaged to undergo natural successional processes (Mitchell, 2005). For example, <15% of beetle-killed forests in Colorado are likely to be actively managed (Collins et al., 2011). Thus, we need to better understand the consequences to stand regeneration of leaving a portion of the MPB attacked landscape unmanaged.

The overall goal of this study was to examine the regeneration potential of lodgepole pine stands post-MPB attack, focusing on a region where MPB is a novel disturbance agent. Our main objectives were to: (i) quantify the availability of seedbed types for germination; (ii) measure the abundance of advance regeneration; and (iii) compare lodgepole pine germination and survival (i.e., recruitment) on five seedbed types (i.e., moss, shallow organic, deep organic, decayed wood, and mineral soil). We addressed these objectives among four different stand treatment types that simulated mountain pine beetle attack and associated forest management disturbance (i.e., control, moderate intensity MPB attack, high intensity MPB attack, and salvage harvest) in the Upper Foothills of western Alberta.

2. Materials and methods

2.1. Study area

The study area was located in the Upper Foothills natural sub-region of Alberta (Natural Regions Committee 2006) in lodgepole pine forests near Robb, AB. This region is characterized by pure lodgepole pine forests that are serotinous (Crossley, 1956), along with mixed conifer stands of white spruce (*Picea glauca* (Moench) Voss) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Stand ages in this region are generally younger than 100–120 years old reflecting the regional disturbance regime of relatively frequent stand-initiating wildfire (Beckingham et al., 1996). This area experiences a temperate continental climate where mean daily maximum air temperatures during the growing season range from 16.2 °C in May to 20.6 °C in August. Snow usually covers the frozen ground from the end of October to late April. Mean monthly precipitation from May to August ranges from 57.9 mm to 82.2 mm, with a mean annual precipitation of 562.4 mm, of which approximately 75% falls as rain. The study stands were approximately 110–120 years old, and were located on brunisolic gray luvisolic soils. The study area was classified as ecosite UF e1.1 – Pl/green alder/feather moss (Beckingham et al., 1996). The overstory included only lodgepole pine; there were a very few white spruce (*P. glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.)), trembling aspen (*Populus tremuloides* Michx.), and balsam fir (*Abies balsamea* (L.) Mill.) in the lower canopy. The understory was dominated by feather mosses, including *Pleurozium schreberi* (Brid.) Mitt., *Polytrichum commune* Hedw., *Ptilium crista-castrensis* (Hedw.) De Not., and Hylocomium splendens (Hew.) Schimp. Common forbs included *Cornus canadensis* L. and *Linnea borealis* L., common small shrubs included *Rosa acicularis* Lindl. and *Vaccinium myrtilloides* Michx.; *Alnus crispa* (Aiton) Pursh was the dominant tall shrub, and the common graminoid was *Calamagrostis montanensis* (Michx.) Beauv.

2.2. Application of treatments

There were four treatments, each applied to one experimental unit (i.e., stand = 0.48 ha) within each of three blocks in early summer 2009: (i) untreated control (hereafter "Control"), (ii) simulated moderate intensity MPB attack (hereafter "50% kill"), (iii) simulated high intensity MPB attack (hereafter "100% kill"), and (iv)

clear-cut – salvage harvested to simulate a typical management treatment post-MPB attack (hereafter "Salvage"). While MPB selectively kills larger and older trees in an endemic setting, our research was focused on epidemic levels of MPB, which are occurring at unprecedented levels on the landscape. Therefore, we selected targets of 50% kill and 100% kill to capture a gradient of mortality.

We used stem injection application of glyphosate herbicide to chemically girdle individual stems to simulate MPB attack in these treated stands. Glyphosate is a systemic herbicide that kills vegetation by inhibiting the enzyme 5-enolpyruvylshikimate 3-phosphate synthase involved in the synthesis of aromatic amino acids; it rapidly reacts with and is inactivated by most soils (Baylis, 2000). EZ-Ject selective injection herbicide capsules (Glyphosate 0.15 grams per capsule, ArborSystems, Omaha, NE http://www.ez-ject.com/) were injected at a rate of 1 capsule per 5 cm tree dbh per tree for trees 10–20 cm dbh, or 1 capsule per 3 cm dbh per tree for trees > 20 cm, with capsules equally spaced around the circumference of the tree near the base of the bole. In the 100% kill experimental units, all trees $\geqslant$ 10 cm dbh (selected as minimum size of trees attacked by MPB – Safranyik and Carroll, 2006) were injected. In 50% kill stands, because of root-to-root transfer of glyphosate among neighboring trees, every 3rd tree $\geqslant$ 10 cm dbh was injected with glyphosate to achieve the desired rate of 50% overstory mortality. Chemical girdling was completed in the treatment year from June 15–19, 2009.

Salvage harvest operations used a "stump-side processing system" in which a feller-processor unit dropped the tree and then limbed and cut it in sections and laid it on the ground. Then a tracked forwarder moved the logs out of the experimental unit. This system leaves debris and cones distributed onsite to facilitate regeneration and is preferable to feller/buncher/skidder operations for small harvest units, where the latter approach leaves a massive pile of debris in the middle of the unit. Harvest operations were completed by West Fraser Timber Company, with one block being cut at a time between late July and early August in the treatment year (2009). Harvest operations were done at a typical time of year, as there was a lot of active harvest being undertaken in the same area as our timber harvest. There is on average about 60% of logging done in the winter and 40% done in the summer for lodgepole pine in Alberta (Bruce Alexander, personal communication). No site preparation, e.g., scarification or burning, was applied to any of the harvest areas and vegetation was allowed to regenerate naturally for the duration of the study.

2.3. Experimental design

We used a randomized block split-split-plot design to study the influence of the four stand-level simulated MPB and forest management treatment types (described above), five seedbed types, and 3 years on germination and early survival of sowed lodgepole pine seeds. There were three blocks in the study ($\sim$5–10 ha each) and a total of 12 experimental units ($n = 3$ replicate blocks $\ast$ 4 experimental units per block). The four treatments were each applied (as described above) to one experimental unit (i.e., stand = 0.48 ha; 60-m by 80-m) within each block in early summer 2009 using a randomized complete block design. A 10-m $\times$ 10-m grid was overlaid on each stand to facilitate placement of a subset of nine systematically-located sample points that were placed at distances of 20-m (i.e., 2 grid points apart along the 60-m direction of the plot) and 30-m (i.e. 3 grid points apart along the 80-m direction of the plot) from one another. Plots were centered on each of these nine points for sampling the overstory, forest floor thickness, saplings, seedbed availability, natural regeneration, and recruitment rates for the spring-sown seed (minimum distance 20 m apart). At an additional nine randomly selected sampling points

on our grid we established recruitment rate subplots and sampled fall-sown seed recruitment rates (minimum distance 10 m apart).

2.4. Data collection

In summer 2010, we sampled the overstory plant community in 8-m fixed-radius (0.02 ha) circular subplots centered at each of the nine systematic sample points within each stand. Standard forest mensuration data were collected for all trees (i.e., with dbh $\geqslant$ 5 cm and ht > 1.3 m) within each subplot, including species, dbh, and live/dead status. Live status of trees was determined based on a visual assessment of tree crowns: healthy trees had green full crowns, dying trees had crowns with moderate to significant quantities of red needles, and dead trees lacked needles, or if needles were still present they were all red. These data were used to calculate basal area and stem density, broken out by live/dead status (healthy, dying and dead). To estimate canopy cover, hemispherical photographs were taken in the middle of the growing season (mid-July) at each of the nine systematically located sample points using a digital Nikon Coolpix 4500 with FC-E8 fisheye lens. Hemispherical photographs were taken approximately 1.4 m above the forest floor, with the camera leveled on a tripod and the bottom of the camera oriented towards north. We analyzed canopy photographs using SLIM (Spot Light Intercept Model v. 3.01), using batch processing to analyze photos with manual color threshold adjustments by plot to optimize differences between canopy and sky. The program calculated gap fraction, which measures the area of overhead view (in percent) which constitutes canopy gaps, and we subtracted gap fraction from 100 to provide an estimate of canopy cover at each sample point. The thickness of the forest floor (excluding the recent litter fall, or L layer, but including both Fibric and Humic layers – i.e., FH) was measured in each of the four corners of the nine seedling quadrats (quadrats described below). A summary of these forest attributes for the study units is provided in Table 1.

We estimated availability of different seedbed types and quantified advance regeneration for the 12 stands using nine 1-m^2 quadrats centered on the systematically-located sample points. To estimate relative seedbed availability, we estimated percent cover (0–100) of moss, exposed mineral soil, downed dead wood (any decay class), exposed rock, and organic matter/litter within each quadrat. Total cover estimates exceeded 100% because of overlap among the litter recorded within the organic matter seedbed and the other seedbed elements. We counted the number of live tree seedlings (i.e., <1.3 m height) by species. We also conducted an additional census for advance regeneration within each stand; four people surveyed each stand for an hour and tallied the total number of pine seedlings found. We also tallied live tree saplings (i.e., taller than 1.3 m ht and dbh < 5 cm) by species within 4-m radius circular plots centered at the same nine sampling points.

We sowed 100 lodgepole pine seeds at five subplots (one for each seedbed type) at each of nine sample points within each of the twelve stands for each of two seasons: (i) an unstratified set sowed at randomly-selected sample points in the fall before snowfall in 2009 (the year of treatment application) (hereafter 'fall sowed'), and (ii) a cold-stratified set sown at the systematic sample points in the spring of 2010 after the snow had melted (hereafter 'spring sown') ($n = 1080$ seed subplots). We seeded five forest floor seedbed types: (i) exposed mineral soil; (ii) mineral soil covered by a FH layer < 2.5 cm depth (hereafter 'shallow organic'); (iii) mineral soil covered by a FH layer > 2.5 cm depth (hereafter 'deep organic'); (iv) feather moss; and (v) decayed wood (i.e., considerably decomposed wood that was incorporated into the forest floor). When we could not locate naturally-occurring mineral and/or decayed wood seedbed types close to a sample point, we carefully removed the forest floor to expose mineral and decayed wood to create these

Table 1
Mean (±SE) values for stand attributes for the four treatments measured in 2010, which was the first growing season after the treatments were applied and the year in which the first set of germinant measurements were recorded.

Stand treatment	Basal area (m^2 ha^{-1})			Trees (ha^{-1})			Canopy cover (%)	Forest floor (FH) thickness (mm)
	Healthy	Dying	Dead	Healthy	Dying	Dead		
Control	30.0 (1.6)	5.1 (0.8)	16.2 (2.9)	970 (101)	172 (15)	987 (227)	64.1 (1.3)	76.6 (3.1)
50% Kill	20.4 (2.7)	12.8 (1.6)	16.1 (0.9)	574 (114)	331 (15)	894 (93)	61.1 (2.0)	78.7 (4.3)
100% Kill	7.6 (2.8)	20.9 (0.7)	22.9 (3.3)	202 (46)	585 (44)	1220 (267)	60.0 (1.5)	84.7 (3.9)
Salvage	0	0	0	0	0	0	0	64.6 (3.8)

seedbed types. From each sampling point, the nearest location (usually within 5 m) of each seedbed type comprising an area of 10-cm by 10-cm (100 cm^2) was chosen for seeding. This sowing intensity provided each seed 1 cm^2 in which to germinate – which we think is sufficient for it to grow for the first season before there would be any significant competition with its germinant neighbors. Seeds were sprinkled on the surface to mimic the effects of natural wind dispersal that would occur after cones opened and were not caged to exclude predators because we wanted to mimic the natural conditions for recruitment within these stands. The lodgepole pine seed we used was collected from the seed zone of the study area by the Alberta Tree Improvement and Seed Centre, Smoky Lake, AB, and originated from seed zone UF1.4 and had a stratified germination rate of 65% (Donna Palamarek personal communication). Unseeded control subplots were also established on whatever seedbed was present at each of the nine systematically located sampling points in each stand to assess any background recruitment occurring from natural seed rain in the area. We counted the number of lodgepole pine germinants within each seedbed type and control subplot bi-weekly throughout the summer of 2010. In June 2011 and July 2012 we revisited the plots once and counted the number of germinants within each seedbed type and control subplot.

2.5. Statistical analyses

To assess germination and survival rates (hereafter 'recruitment' rates), we calculated percent recruitment as the number of germinants (surviving at a given point in time) divided by the number of sown seeds within each seedbed type subplot. We used a three-way repeated measures ANOVA (Proc Mixed) to test for significant (alpha = 0.05) effects of treatment type, seedbed type, year, and their interactions on recruitment using data on the % surviving germinants from the last visit of the growing season in 2010 and from the single visits in 2011 and 2012. This was done for the fall- and spring-sown sets separately. Analysis of residuals and normal probability plots revealed non-constant variance and lack of normality for juvenile recruitment, so these data were logit transformed prior to analysis. When significant main effects were detected, we used post-hoc linear contrasts to make pairwise comparisons among seedbed types within stand treatment types, between stand treatment types for a given seedbed type, and compared them within and among years, using Bonferroni-adjusted P-values (family-wise alpha = 0.05) (Proc Mixed). SAS software (version 9.2 (32 bit); SAS Institute Inc., Cary, North Carolina. ©2000) was used for all analysis.

3. Results

3.1. Seedbed composition

The forest floor seedbed was dominated by feather mosses and litter for all the stand treatment types except for the salvage harvested areas, which were dominated only by litter (Table 2). All

Table 2
Mean (±SE) seedbed availability (% of ground surface) for the four treatment types.

Treatment	Litter (%)	Mineral (%)	Moss (%)	Wood (%)[a]
Control	55.4 (2.9)	0.1 (0.1)	72.6 (4.7)	10.5 (1.6)
50% Kill	57.0 (3.4)	0 (0)	58.2 (4.3)	13.9 (3.0)
100% Kill	63.7 (3.7)	0 (0)	49.9 (5.7)	8.9 (1.5)
Salvage	89.2 (2.1)	1.6 (1.1)	1.3 (0.5)	8.4 (1.1)

[a] This includes both non-decayed and decayed wood.

four stand treatment types had much lower cover of downed wood compared with feather moss and litter (Table 2). Exposed mineral soil cover was very low in all stand treatment types, although the salvage logged stands had the highest cover of mineral soil (Table 2).

3.2. Advance regeneration

There was minimal natural advance regeneration in the study sites, with very low quantities of seedlings. There was a single lodgepole pine seedling located on a squirrel midden in one quadrat in a 100% kill stand. We only counted four juvenile aspen within quadrats: three in 100% kill stands and one in a 50% kill stand. No statistical analysis could be conducted on the seedling data because of low sample sizes. Saplings of aspen, balsam fir, and white spruce existed in some of the stand treatment types, but mean sapling counts were very low in all stand treatment types (Table 3). There were no lodgepole pine saplings in any of the 4-m^2 radius sapling plots and in the pine seedling/sapling census we saw a range of only 0–5 seedlings/saplings per stand, which translates to a density of 0–10.4 understory pine seedlings/saplings per ha.

3.3. Recruitment

No tree seedlings naturally recruited into the control (i.e., unsowed) subplots.

3.3.1. Recruitment from fall-sown seeds

Recruitment rates differed among the stand treatment types and among the 3 years for the fall-sown seeds, but the only significant interaction was between seedbed type and stand treatment type (Table 4). Comparing among the five seedbed types within

Table 3
Mean number of saplings (taller than 1.3 m ht and dbh < 5 cm) per 50 m^2 plot within each treatment type (range of counts provided in parentheses).

Treatment	Sapling count[a]				
	ABBA	PICO	PIGL	POTR	Total
Control	0	0	0.07 (0–2)	0	0.07 (0–2)
50% Kill	0.04 (0–1)	0	0.07 (0–1)	0.41 (0–9)	0.52 (0–9)
100% Kill	0.11 (0–2)	0	0	1.89 (1–33)	2 (0–33)
Salvage	0	0	0	0	0

[a] ABBA is balsam fir, PICO is lodgepole pine, PIGL is white spruce, POTR is aspen.

Table 4
Results (P values) of repeated measures ANOVAs testing for the effects of seedbed type, stand treatment type, year, and the interactions among them on recruitment rates for fall- and spring-sown seed. Significant P-values are highlighted in bold.

Season sowed	Seedbed	Treatment	Year	Seedbed * treatment	Seedbed * year	Treatment * year	Seedbed * treatment * year
Fall	**<0.0001**	**0.01**	**0.02**	**<0.0001**	0.16	0.70	1.0
Spring	**<0.0001**	**0.004**	**0.0004**	**<0.0001**	**0.0009**	0.31	1.0

stand treatment types, there were no significant differences in recruitment rates among the seedbed types within the control treatment type, but there were in the other three stand treatment types (Fig. 1a). In the 50% kill stand treatment type, moss and deep organic seedbed types had significantly lower recruitment rates than the mineral soil, shallow organic, and decayed wood seedbed types (Fig. 1a). In the 100% kill stand treatment type, moss had the

lowest recruitment rate, but it did not significantly differ from deep organic or decayed wood (Fig. 1a). The mineral soil seedbed type had the highest recruitment rate in the 100% kill stand treatment, but was not significantly different than decayed wood. In the salvage logged stand treatment type, mineral soil had the highest recruitment rate, differing from all the other seedbed types (Fig. 1a). Comparing among years for all seedbed types combined, the percent of seed sown in fall 2009 that germinated and survived was highest in 2010, intermediate in 2011, and decreased to the lowest rates in the third year of the study (Fig. 1b).
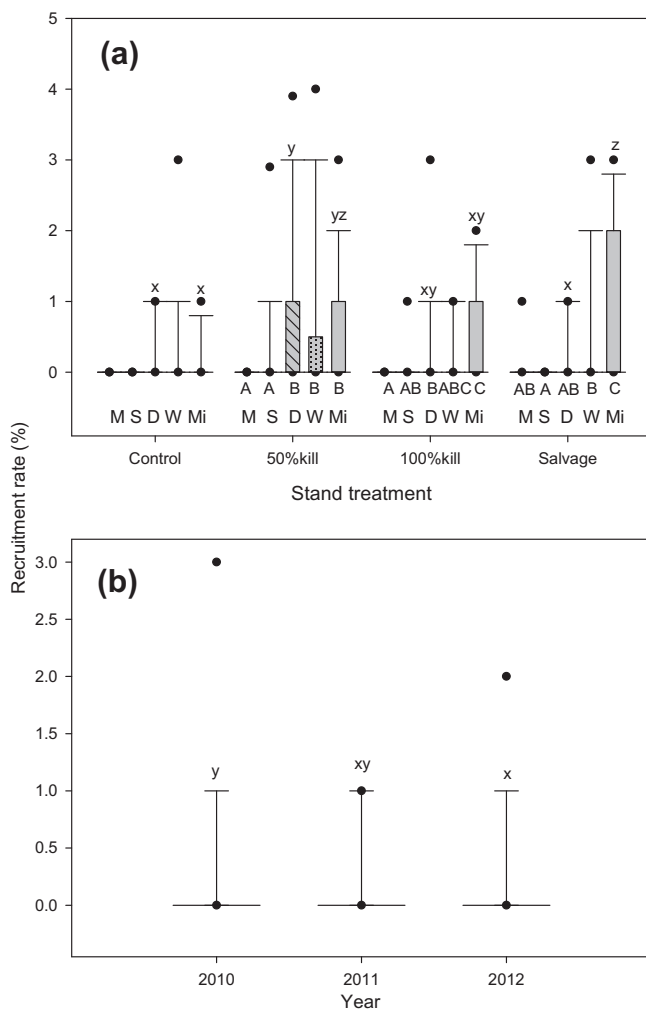
3.3.2. Recruitment from spring-sown seeds

Patterns in recruitment rates of germinants from the spring-sown seeds differed among the stand treatment types and among the years, with significant interactions between seedbed and both stand treatment type and year (Table 4). There were significant differences among the seedbed types for all four stand treatment type types (Fig. 2a). In the control stand type, moss had the lowest recruitment rate, although it was not significantly different than the rate for the deep organic seedbed; decayed wood had the highest recruitment rate, although it was not significantly different than the mineral soil rate (Fig. 2a). In the 50% kill stand treatment, moss again had the lowest recruitment rate, although it was not significantly different than the shallow organic seedbed type (Fig. 2a). Mineral soil had the highest recruitment rate, but this was not significantly different from the recruitment on the decayed wood seedbed type (Fig. 2a). In the 100% kill stand treatment type there was a clear separation into two recruitment groups; moss and the two organic seedbeds had significantly lower recruitment rates than the decayed wood and mineral soil seedbed types (Fig. 2a). In the salvage logged stands, there was also a clear pattern of the highest recruitment rates on decayed wood and mineral soil, but with the two organic seedbed types having intermediate recruitment rates that were significantly higher than for the moss seedbed (Fig. 2a).

Comparing each of the five seedbed types across stand treatment types, there were only significant differences in the decayed wood and mineral soil seedbed type recruitment rates (Fig. 2a). For decayed wood, recruitment rate was significantly higher in the salvage logged stands compared with intermediate rates in the 100% kill stands, and the lowest recruitment rates in the control and 50% kill stand types (Fig. 2a). Mineral soil seedbed recruitment was significantly higher in the salvage logged stand treatment type compared with the other three stand treatment types (Fig. 2a).

There were significant differences among years for the seedbed types for the spring-sown seeds (Fig. 2b). In all 3 years, the decayed wood and mineral soil seedbed types had the highest recruitment rates (Fig. 2b). The percent of sown seed that germinated and survived to the end of 2010 and then 2011 was intermediate on the organic seedbed types and lowest on the moss seedbed, although not significantly lower than the deep organic seedbed type in 2010. Survival to the end of 2012 was similarly low for the moss and two organic seedbed types. Comparing among years for the seed originally sown in 2009, there were only significant differences in recruitment rates for the decayed wood and mineral soil seedbed types, which were both significantly lower in 2011 and 2012 compared with 2010 (Fig. 2b).
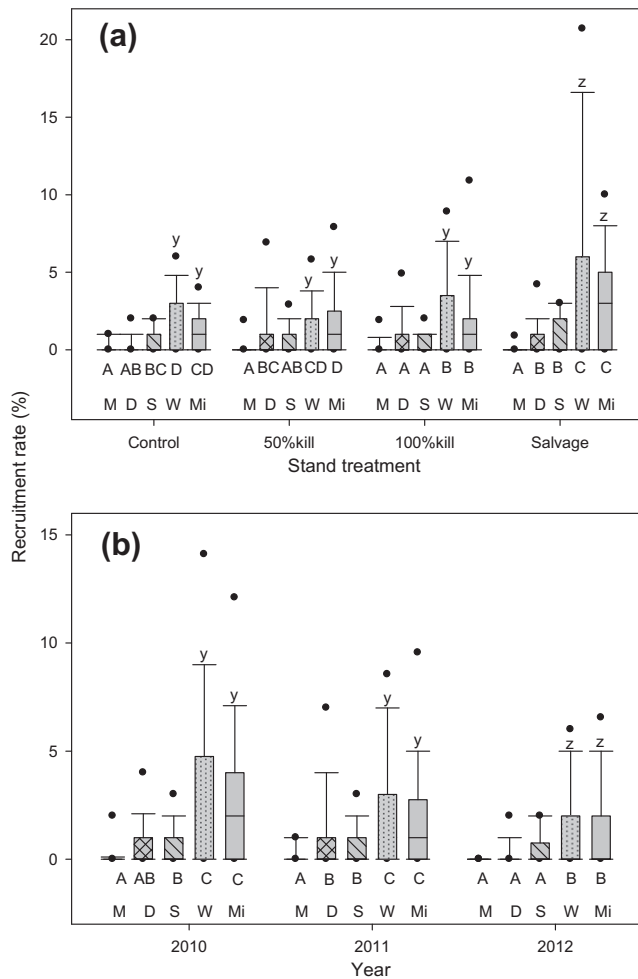

Fig. 1. Recruitment rates (%) for fall-sown seed for: (a) mean % of sown seeds surviving to the end of each year (averaged for 2010, 2011 and 2012) in each of the four stand treatments for each of the five seedbed types (ordered from left to right within each treatment as follows: M: moss, D: deep organic, S: shallow organic, W: decayed wood, and Mi: mineral soil); and (b) overall mean survival (across all stand treatments and seedbed types) to the end of each year. The boundaries of the box are the 25th and 75th percentiles and the line in the middle of the box is the median. Whiskers above and below the box indicate the 90th and 10th percentiles and the dots below and above indicate the 5th and 95th percentiles. In (a) significant differences among seedbed types within a given stand treatment are indicated by capitalized letters (A, B, C) directly below boxplots; significant differences among stand treatments for each seedbed type separately are indicated by lower case letters (x, y, z) above the boxes. In (b) significant differences among years are indicated by lower case letters (x, y, z) above the boxes.

Fig. 2. Recruitment rates (%) for spring-sown seed for (a) mean % of sown seeds surviving to the end of each year (averaged for 2010, 2011 and 2012) in each of the stand treatments for each of the five seedbed types (ordered from left to right within each treatment as follows: M: moss, D: deep organic, S: shallow organic, W: decayed wood, and Mi: mineral soil); and (b) mean survival (across stand treatments) to the end of each year for each seedbed type separately. The boundaries of the box are the 25th and 75th percentiles and the line in the middle of the box is the median. Whiskers above and below the box indicate the 90th and 10th percentiles and the dots below and above indicate the 5th and 95th percentiles. In (a) significant differences among seedbed types within a given treatment are indicated by capitalized letters (*A, B, C*) directly below boxplots; significant differences among treatment types for each seedbed type separately are indicated by lower case letters (*x, y, z*) above the boxes. In (b) significant differences among seedbed types within a given year are indicated by capitalized letters (*A, B, C*) directly below boxplots; significant differences among years for each seedbed type separately are indicated by lower case letters (*x, y, z*) above the boxes.

3.3.3. Mortality of germinants

In 2010, when we monitored germination biweekly, there were only 78 seedbed subplots (7% of total subplots) in which the number of germinants declined by more than 1 between the early summer surveys and the last survey at the end of August. Thus, we did not observe large numbers of germinants that germinated and then died.

4. Discussion

We are unaware of any previous studies that have compared the effects of mountain pine beetle and associated forest management on lodgepole pine recruitment experimentally *in situ* using a direct seeding experiment, and this the first study we are aware of that examines the potential for regeneration in newly invaded stands in MPB's expanded range east of the Canadian Rockies.

While we did not achieve our targets of 50% and 100% kill overstory mortality, the treatments did result in a gradient of decreasing basal area of healthy trees from the control to the 50% (67% of control) and 100% kill (25% of control) stands. Thus our treatments were effective in capturing a gradient of mortality that would be associated with MPB attack. These findings were also supported by evidence of decreased sapflow conductivity in glyphosate-injected trees in a paired hydrology study that was conducted on our study sites (Piña 2012). Therefore, our simulated MPB kill treatments represent two different intensities of MPB mortality (moderate and high) that are likely to occur during epidemic levels of MPB attack.

We did not observe natural recruitment of seedlings for any of the stand treatment types. Our findings are consistent with Astrup et al. (2008) who found limited natural regeneration even 10 years after MPB attack in BC, which they attributed to the intact feather moss-dominated seedbed. An intact feather moss layer in our stands is likely contributing to the low levels of recruitment we observed. Our results differ with Collins et al. (2011) who found that during an MPB outbreak in Colorado, seedlings established in nearly all of the attacked stands they sampled and contributed to the future stand development. However, the seedbed in those sites was comprised of a relatively thin forest floor with <25% herbaceous cover and no moss, which likely contributed to the relatively high seedling recruitment (Collins et al., 2011). We also found no natural recruitment in the salvage logged stands where many of the cones on the ground had opened (personal observation); this suggests that seedbed availability is likely a limiting factor for natural regeneration in the short term. A study by Johnstone (1976) showed lodgepole pine recruitment continued for up to 11 years after logging and scarification in west-central Alberta, with recruitment peaking 6 years after harvest. Thus, recruitment in the salvage logged stands may increase in the coming years.

Our direct seeding experiment allowed us to compare regeneration potential among stand treatment and seedbed types over time without seed rain being a limiting factor. While we did not measure abundance of cones among the treatments, a companion study examining the openness of serotinous cones visible within the canopy in these stands observed that the mature pine trees were cone bearing, and the majority of cones were closed, with no differences in cone openness among the treatments (McIntosh unpublished data). The fall- and spring-sown seeds showed similar patterns in terms of relative differences in recruitment rates over time; germination peaked in the first year (2010) and there was a decline in the survival of these germinants over the 3 year time period. The relatively low recruitment rates we observed are not unusual compared to those found in other boreal field-based germination studies (e.g., Berger, 2002; Purdy et al., 2002).

In general, we found that recruitment rates for the fall-sown seeds were much lower across seedbed and stand treatment types compared with the spring-sown seeds. This could be due to predation, as suggested by Wright et al. (1998) who found the same decline in recruitment rates for overwintered seeds. However, Radvanyi (1971) found higher seed predation in the summer compared with the winter in lodgepole pine clearcuts in central Alberta, suggesting that summer predation may have also contributed to the low germination rates in our study for both sets of sown seed. Additionally, there is potential for herbivory of germinants to have occurred, as exclusion of herbivores has been shown to increase emergence and survival of pine germinants (e.g., – eastern white pine germinants Cornett et al., 1998). However, high levels of herbivory seem unlikely given that most of the germinants that we monitored biweekly in 2010 were still present at the end of the season. The decreased recruitment may also have resulted from

seed movement from the recruitment subplots prior to recruitment, as the snow melting in the spring could have shifted the seeds, especially on the mineral and decayed wood seedbeds, which had relatively smooth surfaces compared with the other three seedbed types. However, this seems unlikely as we did not observe any germinants in areas adjacent to our recruitment subplots. Our findings suggest that if seeding was to be used as a reforestation strategy in these lodgepole pine stands, that it would be best to disperse seed in the spring rather than the fall, even though the latter is more representative of natural dispersal patterns after fire (Astrup et al., 2008).

While the absolute recruitment rates for the spring-sown seeds were higher than for the fall-sown seeds, both showed similar patterns in terms of relative differences in recruitment rates among seedbed types; we consistently found that decayed wood and mineral soil seedbed types had higher recruitment rates than the organic and moss seedbed types did. While forest floor feather mosses have been shown to be positively associated with recruitment of boreal conifers (e.g., Parker et al., 1997), our study showed the opposite for lodgepole pine; the moss seedbed type had consistently no or low recruitment across treatment types. Thus, the potential benefits that mosses can confer to seed, such as decreased vascular plant competition and maintaining a consistent moisture supply (Munier et al., 2010), did not appear to be beneficial to pine regeneration in these stands. In a lodgepole pine seeding experiment in BC, organic seedbeds had higher recruitment rates than moss, but they did not compare these seedbeds with mineral soil (Wright et al., 1998). Given the high rates of germination on organic seedbeds, Wright et al. (1998) suggested mineral soil was not required for good regeneration levels, but that a moderate level of ground disturbance to remove the moss layer would greatly improve seedling establishment. Other studies have also suggested that shallower organic layers were more favorable than deeper organic seedbeds (Greene et al., 2007); however, we found little evidence of this, except for higher recruitment of fall-sown seed for the shallow organic versus the deep organic and moss seedbed types in the 50% kill stand treatment type. Our finding that decayed wood and mineral soil were the most favorable seedbeds is consistent with other studies that have shown these to be the most favorable seedbeds for lodgeople pine germination (Lotan and Perry, 1983; Landhäusser, 2009). Thus, given the generally low abundance of both exposed mineral soil and decayed wood, ground disturbance that exposes mineral soil and/or decayed wood would likely greatly improve recruitment rates in these stands.

Both the fall- and spring-sown seeds also showed similar patterns in terms of relative differences in recruitment rates among stand treatment types; we observed the lowest rates of recruitment in control stands, intermediate recruitment rates in the simulated MPB attack stands and highest rates in the salvage logged stands, particularly for the most favorable seedbeds, mineral soil and decayed wood. In a study in Colorado, new seedling recruitment was four times higher in salvage logged stands, compared with unsalvaged MPB attacked stands (Collins et al., 2011); this was attributed to a decreased density of competing herbaceous vegetation and reduced organic depth. Greene et al. (2009) showed broad consensus that initial survivorship in forest gaps for boreal tree species was highest on mineral soil, humus, and well-rotted logs, and suggested similar patterns for intact forests. This pattern is consistent with our findings of highest recruitment levels on the decayed wood and mineral seedbeds in the salvage logged stands, with a gradient of decreasing recruitment on these seedbeds in the MPB and control stand treatment types. In contrast to our findings, LePage et al. (2000) found regeneration of lodgepole pine in partially-disturbed stands was best on rotten wood, and interestingly, regeneration on mineral soil was very poor; however they had very low sample sizes for lodgepole pine. Our findings suggest that recruitment of lodgepole pine will be higher in stands that are salvage logged, compared with MPB-attacked stands that are left unsalvaged.

Our findings of differences in recruitment rates for decayed wood and mineral soil among stand treatment types suggests that other factors beyond what we measured are also contributing to the variable recruitment rates among stand treatment types. Microclimatic differences among the stand treatment types may also be contributing to these patterns. We expect that as the attacked stands drop their needles and branches and transition to grey attack, the increase in light may lead to an increased pulse in regeneration of shade-intolerant pine, as has been proposed for regeneration in other regions (Axelson et al., 2009; Kayes and Tinker, 2012). Interestingly, other studies have suggested that light is not the primary factor determining regeneration (e.g., Stuart et al., 1989; Williams et al., 1999). Rather than light limitation, drought has been identified as a primary factor leading to mortality of pine seedlings (e.g., Despain, 2001), with soil moisture and microclimate considered the limiting factors for lodgepole pine natural regeneration (Stuart et al., 1989). A companion study adjacent to our research sites examined patterns in soil moisture (at 5 cm depth in the mineral soil) among the stand treatment types in the Summer of 2010 and found a gradient of moisture from the driest soil moisture conditions in the control stand treatment type, with a trend of increasing soil moisture in the 50% kill (10% greater than the control), and 100% kill (13% greater than the control) stand treatment types, with the salvage logged stands being the wettest (33% greater than the control) (Piña 2012). This gradient of increasing soil moisture associated with increasing intensity of disturbance could also be contributing to the overall increase in recruitment in the most favorable seedbed types, especially given that the canopy cover was relatively consistent between the MPB and control stand treatment types. However, we also recognize that soil moisture per se is not particularly relevant for many of the seedbed types. Rather, it is the moisture in the microsite where the seed is sitting that is important; if the mineral soil is moist but the seed is sitting in a dry surface duff layer and cannot get its root into that moisture then it will not survive. The patterns of increasing recruitment levels in the salvage logged stands for the mineral and decayed wood seedbed types suggests that both seedbed and additional factors that we did not explicitly study, such as soil moisture, are important factors in the regeneration of lodgepole pine in these stands.

Regardless of changes in environmental factors influencing regeneration, an increase in availability of favorable seedbeds is critical for successful recruitment in these forests. Across stand treatment types, there was a scarcity of favorable seedbeds for lodgepole pine recruitment. Even in the salvage logged stands where we had the most soil disturbance occur, mineral soil covered <2% of the available seedbed, and there was a maximum of 14% wood, much of which was not yet decayed (personal observation). Thus, unsalvaged MPB killed stands may lack the ground disturbance required for natural regeneration of lodgepole pine (Mitchell, 2005). As the stand breaks up and trees drop to the ground, soil disturbance should increase, creating additional mineral seedbeds. However, in a Colorado MPB attack, there were no differences between fine or coarse DWM loads in uninfested stands and stands with current or recent (up to 7 years prior) MPB attack (Klutsch et al., 2009). Simard et al. (2011) found no differences in surface fuel biomass among unattacked, red, and grey stages of MPB attack. There will be an as yet unknown time lag between when trees are killed and they fall and disturb the soil; MPB-killed trees in central BC did not start to fall until 8 years after they died (Lewis and Thompson, 2011). It seems unlikely that there will be a pulse of decayed wood or mineral soil available as seedbeds in the short term after MPB attack.

5. Conclusions

Our findings of minimal advance regeneration, no natural recruitment post-attack, and the highest recruitment rates on mineral soil and decayed wood, which were scarce across all four stand treatment types and declined over time, suggest that significant silvicultural intervention will be required to supplement regeneration if the goal is for the post-MPB attacked forest to be stocked to lodgepole pine. For attacked forests similar to those in our study that are left unmanaged, which may comprise a large portion of the landscape depending on the magnitude of MPB outbreak in Alberta, it appears that regeneration towards a replacement forest will be slow, owing in part to the lack of both advance regeneration and low availability of suitable seedbed types and associated environmental factors. Another potential concern may be that by the time favorable seedbed types are more available for germination, seed may have already been released from the cones, although Teste et al. (2011a) showed a sustained seed rain even 9 years after MPB attack. Future research is needed that monitors recruitment and longer-term survival of seedlings in attacked forests as they transition to grey attack and eventually fall to the ground in order to better predict the future successional pathway of MPB-disturbed stands that lack additional anthropogenic or natural wildfire disturbances.

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